

Plant Sexual Systems and a Review of the Breeding System Studies in the Caatinga, a Brazilian Tropical Dry Forest

ISABEL CRISTINA MACHADO^{1,*}, ARIADNA VALENTINA LOPES¹ and MARLIES SAZIMA²

¹*Departamento de Botânica—CCB—Universidade Federal de Pernambuco, 50372-970, Recife-PE, Brazil and*

²*Departamento de Botânica—IB—Universidade Estadual de Campinas, 13083-970, C.P. 6109, Campinas-SP, Brazil*

Received: 19 May 2005 Returned for revision: 16 August 2005 Accepted: 27 October 2005 Published electronically: 23 December 2005

• **Backgrounds and Aims** The reproductive biology of a community can provide answers to questions related to the maintenance of the intraspecific pollen flow and reproductive success of populations, sharing and competition for pollinators and also questions on conservation of natural habitats affected by fragmentation processes. This work presents, for the first time, data on the occurrence and frequency of plant sexual systems for Caatinga communities, and a review of the breeding system studies of Caatinga species.

• **Methods** The sexual systems of 147 species from 34 families and 91 genera occurring in three Caatinga areas in north-eastern Brazil were analysed and compared with worldwide studies focusing on reproductive biology of different tropical communities.

• **Key Results** The frequency of hermaphrodite species was 83.0 % (122 species), seven of these (or 4.8 % of the total) being heterostylous. Monoecy occurred in 9.5 % (14) of the species, and andromonoecy in 4.8 % (seven). Only 2.7 % (four) of the species were dioecious. A high percentage of hermaphrodite species was expected and has been reported for other tropical ecosystems. With respect to the breeding system studies with species of the Caatinga, the authors' data for 21 species and an additional 18 species studied by others ($n = 39$) revealed a high percentage (61.5 %) of obligatory self-incompatibility. Agamospermy was not recorded among the Caatinga studied species.

• **Conclusions** The plant sexual systems in the Caatinga, despite the semi-arid climate, are similar to other tropical dry and wet forest communities, including those with high rainfall levels, except for the much lower percentage of dioecious species. The high frequency of self-incompatible species is similar to that reported for Savanna areas in Brazil, and also for dry (deciduous and semideciduous) and humid tropical forest communities.

Key words: Sexual systems, breeding systems, dry forests, Caatinga, north-eastern Brazil.

INTRODUCTION

The reproductive biology of tropical species has been studied in order to understand the mechanisms of gene flow and speciation in plant communities (Baker, 1959; Federov, 1966; Bawa, 1974, 1980; Bawa *et al.*, 1985; Bawa and Hadley, 1990; Gibbs, 1990; Ibarra-Manríquez and Oyama, 1992; Bullock, 1995). The types and frequencies of sexual systems, particularly dioecy, have received attention in studies of tropical, temperate and arctic floras (Bawa, 1980; Flores and Schemske, 1984; Bullock, 1985; Fox, 1985; Steiner, 1988; Renner and Ricklefs, 1995; Oliveira and Gibbs, 2000). The characteristics of flowers and fruits, and the pollination and sexual systems have also been related to dynamic and successional processes (Ibarra-Manríquez and Oyama, 1992).

Studies on the sexual and breeding systems of tropical forests and their ecological relationships have focused particularly on the Neotropics: Costa Rica (Bawa, 1974; Bawa *et al.*, 1985; Kress and Beach, 1994; Wesselingh *et al.*, 1999); Mexico (Bullock, 1985; Ibarra-Manríquez and Oyama, 1992; Tabla and Bullock, 2002); Panama (Croat, 1979); and Venezuela (Ruiz-Zapata and Arroyo, 1978; Sobrevila and Arroyo, 1982; Enrech *et al.*, 1988; Ramírez and Brito, 1990; Ramírez *et al.*, 1990). In Brazil, studies on this subject are found for Savanna ('Cerrado') areas (Saraiva *et al.*, 1996; Oliveira and Gibbs, 2000), coastal

dunes (Ormond *et al.*, 1991; Matallana *et al.*, 2005) and Atlantic forest species (Silva *et al.*, 1997). Community studies in other biogeographical areas include the Mediterranean region (Dafni and O'Toole, 1994) and south-east Asia (Kato, 1996; Momose *et al.*, 1998). However, more studies are needed in order to determine whether different sexual patterns occur among the diverse plant communities.

The Caatinga is a semi-arid vegetation, occurring only in Brazil, almost exclusively in the north-eastern region (Sampaio, 1995; Aguiar *et al.*, 2002; MMA, 2002). It is the fourth largest vegetation type in Brazil, after the Amazonian forest, the Cerrado, and the Atlantic forest (Aguiar *et al.*, 2002), covering 734 478 km² (MMA, 2002). It comprises approx. 82 000 km² (82.88 %) of the state of Pernambuco (Hueck, 1972), which in turn is almost 50 % of the north-eastern region and 8.6 % of the country. Recently the Caatinga was recognized as one of 'Earth's last wild places', and was classified as one of the 37 'Wilderness Areas of the World' (Gil, 2002). The Caatinga is a tropical dry forest and scrub vegetation, occurring in markedly seasonal areas with low rainfall levels (e.g. 500–750 mm year⁻¹), which are irregularly distributed through the year (3–5 months), with annual temperatures averaging 23–27 °C. Rainfall irregularity causes a hydric deficit during a large part of the year (drought periods) (for details, see Sampaio, 1995; Rodal and Melo, 1999).

Despite its great extent and importance, few studies with ecological information are available, and there is a notable

* For correspondence. E-mail imachado@ufpe.br

lack of publications focusing on the biology and the dynamics of its species (for a review, see Leal *et al.*, 2003). Studies on the plant sexual systems of Caatinga species are scarce and focus mainly on individual species (Pinheiro *et al.*, 1991; Vogel and Machado, 1991; Lewis and Gibbs, 1999; Locatelli and Machado, 1999; Machado and Sazima, 1995; Kiill and Ranga, 2000*a, b*, 2003; Quirino and Machado, 2001; Machado *et al.*, 2002; for a review, see also Machado, 1996 and Machado and Lopes, 2002).

The Caatinga areas are suffering increasing anthropic destruction which results in loss of native fauna and flora (Sampaio, 1995; MMA, 2002). As a consequence, the flora and the physiognomy of the vegetation are being markedly altered, and reduced to small fragments, before basic biological or ecological studies are carried out. A broad knowledge of plant reproductive biology may be essential for the maintenance of the biodiversity of fragmented areas in the tropics (Bawa, 1990) and for management projects in this ecosystem.

This work presents general data on the occurrence and frequency of plant sexual systems for Caatinga communities, and includes a review of breeding system studies of Caatinga species. These data complement the study of Machado and Lopes (2004), which reports on floral traits and pollination systems of species of the same Caatinga communities.

MATERIALS AND METHODS

Study sites and species

The study was mainly carried out with species occurring in three semi-arid areas situated in the municipalities of Alagoinha, Buíque and Serra Talhada, located in the rural zone of Pernambuco state, north-eastern Brazil (see fig. 1 in Machado and Lopes, 2004). The areas have different physiognomies, and floristic and phytosociological surveys are available in Ferraz *et al.* (1998); Rodal *et al.* (1998) and Figueiredo *et al.* (2000).

The first area, called Sítio Riacho, is located in the municipality of Alagoinha-PE (8°27'S and 36°46'W), comprises about 80 ha, is at an altitude of 762 m a.s.l. and is 200 km from the coast. The number of dry months varies from five to seven, the mean annual temperature is 22 °C and the precipitation approx. 550 mm (Griz and Machado, 2001). The vegetation is a dense shrubby Caatinga (Egler, 1951).

The second area is a Brazilian National Park located in the Catimbau valley, in the municipality of Buíque-PE (8°67'S and 37°11'W), approx. 285 km from the coast. The altitude ranges from 800 to 1000 m a.s.l., the mean annual precipitation and temperature are, respectively, 1095.9 mm (mostly concentrated between April and June) and 25 °C (SUDENE, 1990). The vegetation is very unusual with plant species not found in other Caatinga areas, some of them typical of 'Campo Rupestre' vegetation (Rodal *et al.*, 1998).

The third and most inland area (approx. 700 km from the coast) is Fazenda Saco, an experimental station of the

Agricultural Research Company of Pernambuco (IPA), located in the municipality of Serra Talhada-PE (7°59'S and 38°19'W). The altitude of the area is about 600 m a.s.l., the mean annual precipitation is around 650 mm (concentrated between January and May) with a dry period between June and December. The mean annual temperature is 26 °C (Machado *et al.*, 1997). The vegetation is dominated by shrubs 3–4 m tall with a few trees reaching 15 m high (Ferraz *et al.*, 1998). For a more detailed description of each study site see Machado and Lopes (2004).

Sexual systems

The sexuality of the flowers of 147 species was determined directly in the field, from herbarium specimens or from literature. Field trips were made five to six times per year, each one lasting 3–5 d, from January 1994 to September 2002. In most cases, only the morphological expression was considered (without performing breeding system experiments), thus functional dioecy was not considered. The species were classified as hermaphrodite (distinguishing those which were heterostylous), monoecious, andromonoecious or dioecious. Voucher specimens are deposited in the Herbarium of the Universidade Federal de Pernambuco (UFP).

Breeding system studies

With regard to the breeding system studies of Caatinga species, the review provides data for 39 species (the authors' data for 21 species, and an additional 18 species studied by others). Information on natural fruit-set (control), cross-pollination, spontaneous and/or hand self-pollination are included, and these are discussed in relation to other ecosystems. For two species [*Angelonia cornigera* (Scrophulariaceae) and *Waltheria rotundifolia* (Sterculiaceae)] manual pollinations were made to supplement information given in previous studies by the authors.

RESULTS AND DISCUSSION

Habit and sexual systems

In total, the habits and sexual systems of 147 species, including various life forms (43.9 % shrubs, 18.9 % trees, 18.2 % herbs, 13.5 % lianas, 4.1 % epiphytes and 1.4 % herbaceous climbers), distributed in 34 families and 91 genera were studied (Table 1). This number represents approx. 16 % of the known Caatinga plant diversity (MMA, 2002; for a review, see Leal *et al.*, 2003), an ecosystem where the shrubby habit predominates (Ferraz *et al.*, 1998; Rodal *et al.*, 1998; Figueiredo *et al.*, 2000).

The frequency of hermaphroditic species was 83 % (122 species), seven of these (or 4.8 % of the total) heterostylous. Monoecy occurred in 9.5 % (14) of the species, followed by andromonoecy in 4.8 % (seven), and dioecy, in only 2.7 %, which was represented by four species: *Clusia nemorosa* (Clusiaceae) (not really typical of Caatinga areas), *Commiphora leptophloeos* (Burseraceae), *Myracrodruon urundeuva* and *Schinopsis brasiliensis* (Anacardiaceae). A high percentage of hermaphroditic species was expected,

TABLE 1. Habits and sexual systems of the studied species from three Caatinga areas in Pernambuco state, north-eastern Brazil

Families and species*	Habit [†]	Sexual system [‡]
ACANTHACEAE (2 genera/4 species)		
<i>Harpochilus neesianus</i> Mart.	S	Hm
<i>Ruellia asperula</i> (Nees) Lindau	H	Hm
<i>Ruellia</i> aff. <i>paniculata</i> L.	H	Hm
<i>Ruellia</i> sp. 1	H	Hm
AMARANTHACEAE (1/1)		
<i>Gomphrena vaga</i>	H	Hm
ANACARDIACEAE (3/3)		
<i>Myracrodruon urundeuva</i> Allemão	T	D [§]
<i>Schinopsis brasiliensis</i> Engl.	T	D [§]
<i>Spondias tuberosa</i> Arruda Cam.	T	A
ANNONACEAE (1/1)		
<i>Rollinia leptopetala</i> R.E. Fries	T	Hm
APOCYNACEAE (3/4)		
<i>Aspidosperma pyrifolium</i> Mart.	T	Hm
<i>Allamanda blancheti</i> A. DC.	L	Hm
<i>Allamanda</i> sp.	S	Hm
<i>Mandevilla tenuifolia</i> (Mikan) Woodson	H	Hm
BIGNONIACEAE (2/2)		
<i>Tabebuia impetiginosa</i> (Mart. ex DC.) Standl.	T	Hm
<i>Anemopaegma</i> sp.	L	Hm
BOMBACACEAE (2/2)		
<i>Pseudobombax marginatum</i> (A. St.-Hil.) A.Robyns	T	Hm
<i>Ceiba glaziovii</i> (Kuntze) K. Schum.	T	Hm
BORAGINACEAE (1/2)		
<i>Cordia globosa</i> (Jacq.) Kunth	S	Ht
<i>C. leucocephala</i> Moric.	S	Ht
BROMELIACEAE (6/8)		
<i>Dyckia pernambucana</i> L.B. Sm.	H	Hm
<i>Billbergia portea</i> Brongn.	E	Hm
<i>Encholirium spectabile</i> Mart. ex Schult.f.	H	Hm
<i>Neoglaziovia variegata</i> (Arr. Cam.) Mez.	H	Hm
<i>Portea leptantha</i> Harms	H/E	Hm
<i>Tillandsia gardneri</i> Lindl.	E	Hm
<i>T. loliacea</i> Mart. ex Schult.	E	Hm
<i>T. streptocarpa</i> Baker	E	Hm
BURSERACEAE (1/1)		
<i>Commiphora leptophloeos</i> (Mart.) J.B. Gillett	T	D
CACTACEAE (5/11)		
<i>Cereus jamacaru</i> DC.	T	Hm
<i>Harrisia adscendens</i> (Gürke) Britton & Rose	HC	Hm
<i>Melocactus bahiensis</i> (Br.et Rose) Werderm.	H	Hm
<i>M. zehntneri</i> (Britton & Rose) Luetzelburg	H	Hm
<i>Opuntia inamoema</i> K. Schum.	S	Hm
<i>O. palmadora</i> Britton & Rose	S	Hm
<i>Pilosocereus cattingicola</i> (Gürke) Byles & G.D. Rowley	T	Hm
<i>P. chrysostele</i> (Vaupel) Byles & G.D. Rowley	T	Hm
<i>P. gounellei</i> (F.A.C.Weber) Byles & G.D. Rowley	S	Hm
<i>P. pachycladus</i> (Werderm.) Byles & G.D. Rowley	T	Hm
<i>P. tuberculatus</i> (Werderm.) Byles & G.D. Rowley	T	Hm
CAPPARACEAE (1/4)		
<i>Capparis hastata</i> L.	S	Hm
<i>C. flexuosa</i> (L.) L.	T	Hm
<i>C. jacobinae</i> Moric. ex Eichler	S	Hm
<i>C. yco</i> (Mart.) Eichler	S	Hm
CLUSIACEAE (1/1)		
<i>Clusia nemorosa</i> G. Mey.	S	D
COMBRETACEAE (2/4)		
<i>Combretum hilarianum</i> D. Dietr.	L	Hm
<i>C. leprosum</i> Mart.	L	Hm
<i>C. pisonioides</i> Taub.	S	Hm
<i>Thilsea glaucocarpa</i> (Mart.) Eichler	S	Hm
CONVOLVULACEAE (4/7)		
<i>Evolvulus</i> sp.	L	Hm
<i>Ipomoea acuminata</i> Baker	L	Hm
<i>Ipomoea</i> sp. 1	L	Hm
<i>Ipomoea</i> sp. 2	L	Hm
<i>Jacquemontia densiflora</i> (Meissn.) Hall.	L	Hm

TABLE 1. Continued

Families and species*	Habit [†]	Sexual system [‡]
<i>Merremia aegyptia</i> (L.) Urb.	L	Hm
<i>Merremia</i> sp.	L	Hm
EUPHORBIACEAE (8/12)		
<i>Acalypha multicaulis</i> Müll. Arg.	S	M
<i>Cnidocolus urens</i> (L.) Arthur	S	M
<i>Croton argyrophylloides</i> Müll. Arg.	S	M
<i>C. sonderianus</i> Müll. Arg.	S	M
<i>Croton</i> sp.	S	M
<i>Dalechampia</i> sp.	HC	M
<i>Euphorbia comosa</i> Vell.	H	M
<i>Jatropha mollissima</i> (Pohl) Baill.	S	M
<i>J. mutabilis</i> (Pohl) Baill.	S	M
<i>J. ribifolia</i> (Pohl) Baill.	S	M
<i>Manihot</i> cf. <i>pseudoglaziovii</i> Pax & K. Hoffm.	S	M
<i>Maprounea</i> aff. <i>guianensis</i> Aubl.	T	M
KRAMERIACEAE (1/1)		
<i>Krameria tomentosa</i> A. St.-Hil.	S	Hm
LAMIACEAE (1/1)		
<i>Hyptis martiusii</i> Benth.	H	Hm
LEGUMINOSAE (15/29)		
<i>Acacia farnesiana</i> (L.) Willd.	S	Hm
<i>Amburana cearensis</i> (Allemão) A.C. Sm.	T	Hm
<i>Anadenanthera colubrina</i> var. <i>cebil</i> (Griseb.) Altschul	T	Hm
<i>Bauhinia acuruana</i> Moric.	S	Hm
<i>B. cheilantha</i> (Bong.) Vogel ex Steud.	S	Hm
<i>B. pentandra</i> (Bong.) Vogel ex Steud.	S	Hm
<i>Caesalpinia ferrea</i> Mart. ex Tul.	T	Hm
<i>C. pyramidalis</i> Tul.	T	Hm
<i>Calliandra aeschynomoides</i> Benth	S	Hm
<i>Chamaecrista cytisoides</i> (Collad.) Irwin & Barneby	S	Hm
<i>Chamaecrista ramosa</i> (Vogel) var. <i>mollissima</i> (Benth.) Irwin & Barneby	S	Hm
<i>Chamaecrista</i> sp. 1	S	Hm
<i>Cratylia mollis</i> Mart. ex Benth.	S	Hm
<i>Erythrina velutina</i> Willd.	T	Hm
<i>Lonchocarpus</i> aff. <i>campestris</i> Benth.	T	Hm
<i>Mimosa lewisii</i> Barneby	S	Hm
<i>M. tenuiflora</i> (Willd.) Poir.	T	Hm
<i>Parapiptadenia zehntneri</i> (Harms) M.P. Lima & H.C. Lima	T	Hm
<i>Periandra coccinea</i> (Schrud.) Benth.	L	Hm
<i>Senna acuruensis</i> (Benth.) Irwin & Barneby	S	Hm
<i>S. angulata</i> (Vogel) Irwin & Barneby	T	Hm
<i>S. chrysocarpa</i> (Desv.) H.S. Irwin & Barneby	S	Hm
<i>S. macranthera</i> (Collad.) Irwin & Barneby	S	Hm
<i>S. martiana</i> (Benth.) H.S. Irwin & Barneby	S	Hm
<i>S. rizzini</i> Irwin & Barneby	T	Hm
<i>S. spectabilis</i> (DC.) var. <i>excelsa</i> (Schrud.) Irwin & Barneby	S	Hm
<i>S. splendida</i> (Vogel) Irwin & Barneby	S	Hm
<i>S. trachypus</i> (Benth.) Irwin & Barneby	S	Hm
<i>Zornia sericea</i> Moric.	H	Hm
MALPIGHIACEAE (5/7)		
<i>Banisteriopsis schizoptera</i> (A. Juss.) B. Gates	L	Hm
<i>Byrsonima gardneriana</i> Juss.	S	Hm
<i>Byrsonima vacciniaefolia</i> Juss.	S	Hm
<i>Byrsonima</i> sp.	S	Hm
<i>Janusia anisandra</i> (Juss.) Griseb.	L	Hm
<i>Heteropteris</i> sp.	L	Hm
<i>Stigmaphyllon paralias</i> Juss.	S	Hm
MALVACEAE (4/5)		
<i>Bakeridesia pickelii</i> Monteiro	S	Hm
<i>Herissantia tiubae</i> (K. Sch.) Briz.	H	Hm
<i>Pavonia humifusa</i> A. St.-Hil.	S	Hm
<i>P. martii</i> Mart. Ex Colla	H	Hm
<i>Sida</i> sp.	H	Hm
ORCHIDACEAE (2/2)		
<i>Cyrtopodium intermedium</i> Brade	E	Hm
<i>Stenorrhynchus lanceolatus</i> (Aubl.) Rich. ex Spreng.	H	Hm
PASSIFLORACEAE (1/4)		
<i>Passiflora foetida</i> L.	L	Hm

TABLE 1. Continued

Families and species*	Habit [†]	Sexual system [‡]
<i>P. luetzelburgii</i> Harms	L	Hm
<i>Passiflora</i> sp. 1	L	Hm
<i>Passiflora</i> sp. 2	L	Hm
RHAMNACEAE (1/1)		
<i>Ziziphus joazeiro</i> Mart.	T	Hm
RUBIACEAE (2/2)		
<i>Coutarea hexandra</i> (Jacq.) K. Schum.	S	Ht
<i>Tocoyena formosa</i> (Cham. & Schltdl.) K. Schum.	S	Hm
SAPINDACEAE (2/2)		
<i>Allophylos quercifolius</i> (Mart.) Radlk.	S	M
<i>Serjania comata</i> Radlk.	L	M
SAPOTACEAE (1/1)		
<i>Bumelia sartorum</i> Mart.	T	Hm
SCROPHULARIACEAE (3/7)		
<i>Angelonia bisaccata</i> Benth.	S	Hm
<i>A. cornigera</i> Hook.	H	Hm
<i>A. hirta</i> Cham.	H	Hm
<i>A. hookeriana</i> Gardn.	S	Hm
<i>A. pubescens</i> Benth.	H	Hm
<i>Bacopa</i> sp.	H	Hm
<i>Stemodia</i> sp.	H	Hm
SOLANACEAE (2/7)		
<i>Nicotiana tabacum</i> L.	S	Hm
<i>Solanum asperum</i> Rich.	S	A?
<i>S. baturitense</i> Huber	S	A?
<i>S. crinitum</i> Lam.	S	A?
<i>S. gardneri</i> Sendtn.	S	A?
<i>S. paludosum</i> Moric.	S	A?
<i>S. variabile</i> Mart.	S	A?
STERCULIACEAE (3/4)		
<i>Helicteres mollis</i> K. Schum.	S	Hm
<i>H. cf. velutina</i> K. Schum.	S	Hm
<i>Waltheria rotundifolia</i> Schrank	S	Ht
TILIACEAE (1/1)		
<i>Luehea</i> sp.	S	Hm
TURNERACEAE (1/2)		
<i>Turnera diffusa</i> Willd. ex Schult.	S	Ht
<i>Turnera</i> sp.	H	Ht
VERBENACEAE (2/3)		
<i>Lantana camara</i> L.	H	Hm
<i>Lippia gracilis</i> Schau.	H	Hm
<i>L. schomburgkiana</i> Schau.	S	Hm
VIOLACEAE (1/1)		
<i>Hybanthus calceolaria</i> (L.) G.K. Schulze.	H	Hm

* The species are listed by family and in alphabetical order.

[†] T, Tree; S, shrub; H, herb; L, liana; E, epiphyte; HC, herbaceous climber.

[‡] Hm, hermaphrodite; Ht, herm. heterostylous; M, monoecious; A, andromonoecious; D, dioecious.

[§] A. V. L. Leite, personal communication.

since this is the most common sexual system in plants (Richards, 1986), and similar percentages have been reported for other tropical ecosystems (Table 2).

The percentage of monoecious species (9.5 %) agrees with the data of some authors (Table 2), but is higher than the values of 4.5–5 % given for Savanna ('Cerrado') communities (Saraiva *et al.*, 1996; Oliveira and Gibbs, 2000), and less than half that found in some tropical evergreen forests. The highest frequency of monoecious species (19.53 %) was reported for a Palm swamp community in Venezuela by Ramírez and Brito (1990) (Table 2), but this value is probably influenced by the predominance of palms in this community. Similarly, in the Caatinga areas studied, the percentage of monoecy can be associated with the high

frequency of Euphorbiaceae species, since 12 of the 14 monoecious species belong to this family (Table 1), one of the three most representative families in this ecosystem.

Andromonoecy in the Caatinga (4.8 %) occurs mainly in Solanaceae species (Table 1), a family in which this sexual system is common (Symon, 1979; Coleman and Coleman, 1982; Anderson and Symon, 1989). Data about andromonoecy for other communities are scarce and available only for dry forest communities and with contrasting frequencies (2 % and 13.6 %) (Table 2).

The proportion of dioecious species in the Caatinga (2.7 %) is much lower than in other tropical ecosystems (Table 2), being comparable with the percentage (3 %) recorded by Barbosa (1997) for understory species of a

TABLE 2. Frequency of sexual systems and self-incompatibility (SI) in species of Caatinga as compared with studies of Neotropical and Paleotropical communities

Studies in tropical communities	Hermaphrodite (%)		Monoecious (%)	Andromonoecious (%)	Dioecious (%)	SI ⁶ (%)
	Monostylous	Heterostylous				
DRY FORESTS*						
Tropical dry forest and scrub vegetation, 'Caatinga', Brazil (this study) ¹	78.2	4.8	9.5	4.8	2.7 ¹ 11 ³ 4.3 ⁴	61.5
Savanna, 'Cerrado', Brazil (Oliveira and Gibbs, 2000) ²	80.0	—	5.0	—	15.0	66
Tropical semi-deciduous forest, Mexico (Bullock, 1985) ¹	67.2	3.0	14.9 ⁷	2.0	13.0 ⁸	76
Tropical deciduous forest, Mexico (Tabla and Bullock, 2002) ¹	70.2	—	17.6	—	12.3	—
Semi-deciduous forest, Costa Rica (Bawa, 1974; Bawa and Opler, 1975) ³	68.0	—	10.0	—	22.0	79.4 (<i>n</i> = 34) ⁹ ; 54 (<i>n</i> = 130) ⁹
Secondary deciduous forest, Venezuela (Ruiz-Zapata and Arroyo, 1978) ¹	54.6	9.1	—	13.6	22.7	54.45
RAIN FORESTS*						
Atlantic forest, Brazil (Silva <i>et al.</i> , 1997) ⁴	78.9	—	8.5	—	12.6	—
Lowland rain forest, Costa Rica (Kress and Beach, 1994) ¹	70.2	—	12.4	—	17.4	50.9
Lowland rain forest, Costa Rica (Bawa <i>et al.</i> , 1985) ³	65.5	—	11.4	—	23.1	82.14 ¹⁰
Tropical rain forest, Mexico (Ibarra-Manriquez and Oyama, 1992) ³	63.0	—	9.0	—	27.0	—
Moist forest, Barro Colorado, Panama (Croat, 1979) ¹	76.0	—	15.0	—	9.0	—
Montane cloud forest, Venezuela (Sobrevila and Arroyo, 1982) ¹	69.45 ^{3,11} 97.44 ^{11,12}	—	—	—	30.55 ³ 2.56 ¹²	26.21 ³ 41.76 ¹²
Tropical palm swamp, Venezuela (Ramírez and Brito, 1990) ¹	77.3	—	19.5	—	3.1	30.77
Montane forest, Jamaica (Tanner, 1982) ³	68.0	—	11.0	—	21.0	12
Lowland mixed dipterocarp forest, Malaysia (Kato, 1996) ⁵	80.5	—	7.3	—	12.2	—
MARINE INFLUENCED VEGETATION*						
'Restinga' (coastal vegetation), Brazil (Ormond <i>et al.</i> , 1991) ¹	75.6	—	14.2	—	10.2	—
'Restinga' (tropical coastal vegetation), Brazil (Matallana <i>et al.</i> , 2005) ¹	75 ¹	—	11 ¹	—	14 ¹ 35 ¹³	—

* Vegetation type as mentioned by the authors.

¹ Including species from all life forms; ² woody species only; ³ trees only; ⁴ trees and shrubs only; ⁵ understorey species only; ⁶ considering hermaphrodite and monoecious species only; ⁷ including 1.6 % of gynomonocious species and 0.3 % polygamomonocious species; ⁸ including 0.6 % of gynodioecious species and 0.1 % of androdioecious species; ⁹ data from Bawa (1974); ¹⁰ SI frequency value varying: 85.71 %, 82.14 % and 81.48 %; ¹¹ including hererostylous and monoecious species according to the authors; ¹² shrubs, herbs and vines only; ¹³ dominant woody species only.

Brazilian Savanna (Cerrado), and by Ramírez and Brito (1990) for a palm swamp community in Venezuela (3.1 %), which included species of all life forms. However, with respect to Cerrado woody species, Oliveira and Gibbs (2000) recorded 15 % of dioecy. If the percentage of dioecy in the Caatinga for only trees and shrubs is analysed, the value would be 4.3 % or approx. 11 % when only trees are considered. These values are still lower than those reported for most dry and humid forests (when comparisons take into consideration the life forms). The percentages of the sexual systems among diverse ecosystems are summarized in Table 2; these include studies in dry and humid areas, some are for woody species only, others with species of every life form. There are no differences among data between dry and humid communities, and there is a tendency for higher percentages of dioecy in studies restricted to woody species. In general, Renner and Ricklefs (1995) estimate the occurrence of approx. 6 % of dioecious species among angiosperms, a rather higher percentage than in the Caatinga.

Dioecy has been related to small generalist insect pollination (Bawa and Opler, 1975; Bawa, 1980; Bawa *et al.*, 1985) and, in fact, three of the four dioecious species recorded here are pollinated by diverse small insects (Machado and Lopes, 2004). However, *Clusia nemorosa* has large and very attractive flowers and offers resin as floral reward for female bees of the tribe Euglossini (Lopes and Machado, 1998). In general, the floral traits and pollination systems recorded by Machado and Lopes (2004) in the same Caatinga communities revealed a low percentage of small generalist flowers, which may explain the low occurrence of dioecy.

Dioecy has also been associated with specialized zoochory (Bawa and Opler, 1975; Bawa, 1980; Bawa *et al.*, 1985). This syndrome is present in two of the dioecious species, *Commiphora leptophloeus* and *Clusia nemorosa*, which have capsules with seeds covered by a reddish aril, thus probably attracting birds, but the remaining two species, *Myracrodunon urundeuva* and *Schinopsis brasiliensis*, have dry, abiotic dispersed fruits. Griz and Machado (2001)

TABLE 3. Data compiled for breeding system of 39 species occurring in Caatinga areas in north-eastern Brazil

Family and species	Habit	Cross-pollination	Spontaneous self	Manual self	Agamospermy	Control	Breeding systems*	Source
AGANTHACEAE								
<i>Harpochilus neesianus</i> Mart.	Shrub	—	—	—	—	12.17 %	SI?	Vogel <i>et al.</i> , 2004
<i>Ruellia asperula</i> (Nees) Lindau	Herb	(16/12) 75.0	(27/10) 37.0	(17/13) 76.5	(10/0) 0	(17/6) 35.5	SC	Machado, 1990; Machado and Sazima, 1995
<i>R. aff. paniculata</i> L.	Herb	(10/10) 100.0	(20/20) 100.0	(10/9) 90.0	(10/0) 0	Ca. 90.0 %	SC	Machado, 1990
BORAGINACEAE								
<i>Auxemma glazioviana</i> Taub.	Tree	Intermorph (26/11) 64.5	(33/30) 0	(32/10) 0	(17/0) 0	(44/54/354) 8.0	SI	Silva and Machado, 1997
<i>A. onocadyx</i> (Fr. All.) Taub.	Tree	Intermorph (56/150) 27.5	(54/79) 0	(28/7) 0	(118/0) 0	(141/40/217) 2.0	SI	Silva and Machado, 1997
<i>Cordia globosa</i> (Jacq.) Kunth	Shrub	Intermorph (20/15) 75.0	(20/0) 0	0	0	Ca. 70.0 %	SI	Machado, 1990
<i>C. leucocephala</i> Moric.	Shrub	Intermorph (20/1) 7.5	(20/0) 0	0	0	Ca. 5.0 %	SI	Machado, 1990
CACTACEAE								
<i>Melocactus zehntneri</i> (Britton & Rose) Luetzelburg	Herb	(15/12) 80.0	(20/17) 85.0	(10/9) 90.0	(10/0) 0	(20/19) 95.0	SC	Locatelli and Machado, 1999
<i>Opuntia palmadora</i> Britton & Rose	Shrub	(30/19) 63.0	(30/21) 70.0	30/23	(20/0) 0	(30/25) 83.0	SC	Locatelli and Machado, 1999
CAPARACEAE								
<i>Capparis hastata</i> L.	Shrub	(23/19) 82.6	(42/0) 0	(42/14) 33.3	(32/0) 0	(141/56) 39.7	SC	Primo, 2004
<i>C. jacobinae</i> Moric ex Eichler	Shrub	(72/51) 17.2	(33/0) 0	(105/1) 0.9	(32/0) 0	(99/21) 21.2	SI	Primo, 2004
COMBRETACEAE								
<i>Combretum leprosum</i> Mart.	Liana	(50/8) 16.0	(50/0) 0	(50/0) 0	(50/0) 0	(100/19) 19.0	SI	Quirino and Machado, 2001
<i>C. pisonioides</i> Taub.	Shrub	(50/10) 20.0	(50/0) 0	(50/0) 0	(30/0) 0	(40/4) 10.0	SI	Quirino and Machado, 2001
CONVOLVULACEAE								
<i>Ipomoea asarifolia asarifolia</i> (Ders.) Roem. & Schult.	Liana	(30/18) 60.0	(30/0) 0	(30/1) 3.0	(30/0) 0	(30/23) 76.0	SI	Piedade, 1998; Kiill and Ranga, 2000a
<i>I. incarnata</i> Choisy	Liana	(30/22) 73.0	(30/0) 0	(30/2) 6.0	(30/0) 0	(30/25) 83.0	SI	Piedade, 1998
<i>I. bahiensis</i> Willd. ex Roem. & Schult.	Liana	(30/17) 56.0	(30/0) 0	(30/0) 0	(32/0) 0	(31/21) 67.0	SI	Piedade, 1998
<i>I. brasiliana</i> Meisn.	Liana	(30/7) 23.0	(30/1) 3.0	(30/0) 0	(32/0) 0	(35/10) 28.0	SI	Piedade, 1998
<i>I. maritima</i> Meisn.	Liana	(30/0) 0	(30/0) 0	(30/0) 0	(30/0) 0	(30/0) 0	SI?	Piedade, 1998
<i>Jacquemonia multiflora</i> (Choisy) Hallier f.	Liana	(30/18) 60.0	(30/1) 3.0	(30/10) 33.0	(30/0) 0	(31/19) 60.0	SC	Kiill and Ranga, 2000b
<i>Merremia aegyptia</i> L. Urban.	Liana	(30/19) 63.0	(30/10) 33.0	(30/13) 43.0	(30/0) 0	(30/25) 83.0	SC	Kiill and Ranga, 2000a
EUPHORBACEAE								
<i>Jatropha gossypifolia</i> L.	Shrub	(40/33) 82.5	—	(40/30) 75.0	—	(100/95) 95.0	SC	Ormond <i>et al.</i> , 1984
<i>J. mollissima</i> (Pohl.) Baill.	Shrub	(20/19) 95.0	—	(20/13) 65.0	(20/0) 0	(20/17) 85.0	SC	Santos <i>et al.</i> , 2005
<i>J. mutabilis</i> (Pohl.) Baill.	Shrub	(20/16) 80.0	—	(20/12) 60.0	(20/0) 0	(20/15) 75.0	SC	Santos <i>et al.</i> , 2005
LEGUMINOSAE								
<i>Caesalpinia calycina</i> Benth.	Shrub	(19/5) 26.3	0	(23/0) 0	—	(3083/393) 12.75	SI	Lewis and Gibbs, 1999
<i>C. pluviosa</i> DC. var. <i>sanfranciscana</i> G.P.Lewis	Tree	—	—	—	—	(100/4) 4.0	SI?	Lewis and Gibbs, 1999
<i>Chamaecrista cytisoides</i> (Collad.) Irwin & Barnely	Shrub	(30/12) 40.0	(37/0) 0	(30/8) 26.6	—	(106/56) 52.8	SC	Silva, 2004
<i>Ch. ramosa</i> (Vogel) var. <i>mollissima</i> (Benth.) Irwin & Barnely	Shrub	(30/18) 60.0	(57/0) 0	(30/15) 50.0	—	(110/22) 20.0	SC	Silva, 2004
<i>Gliricidia sepium</i> (Jacq.) Steud.	Tree	(31/16) 51.6	(36/0) 0	(30/0) 0	(30/0) 0	(30/9) 30.0	SI	Kiill and Drummond, 2001
MALPIGHIACEAE								
<i>Byrsonima gardneriana</i> Juss.	Shrub	(30/28) 93.3	(30/0) 0	(30/0) 0	(30/0) 0	(129/68) 52.7	SI	Bezerra, 2004
<i>Stignaphyllon paralius</i> Juss.	Shrub	(30/26) 88.66	(30/0) 0	(30/0) 0	(30/0) 0	(45/38) 84.4	SI	Bezerra, 2004
MALVACEAE								
<i>Pavonia maritima</i> Mart. ex Cola	Herb	(10/10) 100.0	(20/20) 100	(10/10) 100.0	(10/0) 0	98.0 %	SC	Machado, 1990

TABLE 3. Continued

Family and species	Habit	Cross-pollination	Spontaneous self	Manual self	Agamospermy	Control	Breeding systems*	Source
RHAMNACEAE								
<i>Ziziphus joazeiro</i> Mart.	Tree	(29/9) 31.0	(30/0) 0	(40/7) 15.5	—	(96/15) 15.6	SC	Pinheiro <i>et al.</i> , 1991
SCROPHULARIACEAE								
<i>Angelonia bisaccata</i> Benth.	Shrub	(20/18) 90.0	(10/0) 0	(10/0) 0	(10/0) 0	Ca. 65.0 %	SI	Machado, 1990; Vogel and Machado, 1991
<i>A. cornigera</i> Hook.	Herb	(20/17) 85.0	(15/0) 0	(21/0) 0	(20/0) 0	Ca. 60.0 %	SI	Machado <i>et al.</i> , 2002; this study
<i>A. hirta</i> Cham.	Herb	(20/20) 100.0	(20/0) 0	(20/0) 0	(10/0) 0	Ca. 65.0 %	SI	Machado, 1990; Vogel and Machado, 1991
<i>A. hookeriana</i> Gardn.	Shrub	(15/14) 93.3	(10/0) 0	(10/0) 0	(10/0) 0	Ca. 65.0 %	SI	Machado, 1990; Vogel and Machado, 1991
<i>A. pubescens</i> Benth.	Herb	(20/20) 100.0	(20/20) 100.0	(20/20) 100.0	(20/0) 0	Ca. 100.0 %	SC	Machado, 1990; Vogel and Machado, 1991
STERCULIACEAE								
<i>Melochia tomentosa</i> L.	Shrub	Intermorph (110/108) 98.2 [†]	(120/0) 0	0	0	Ca. 90.0 %	SI	Machado, 1990
<i>Waltheria rotundifolia</i> Schrank	Shrub	Intermorph (20/12) 60.0 [†]	(20/0) 0	(10/0) 0	(10/0) 0	Ca. 65.0 %	SI	Machado, 1990; this study

The values are (number of flowers/fruits) %.

* SC, Self-compatible; SI, self-incompatible.

[†] Intramorph crosses did not result in fruits.

[‡] Result refers to geitonogamy since the species is monoecious.

recorded zoochory for 36 % against 64 % with abiotic dispersed seeds, of the Caatinga species in an area of Pernambuco, a scenario which possibly correlates with the low occurrence of dioecy. A strong association between seed dispersal and dioecy, as well as pollination and other ecological factors was recorded for a rain forest in Mexico (Ibarra-Manriquez and Oyama, 1992).

Another explanation for the reduced percentage of dioecious species in the Caatinga could be the predominance of life forms other than trees (Table 1). Analysis of the growth forms of dioecious angiosperm genera revealed a higher proportion among trees (cf. Bawa and Opler, 1975; Sobrevila and Arroyo, 1982; Bawa *et al.*, 1985; Bullock, 1985; Renner and Ricklefs, 1995), and a comparison of the percentages of dioecious species among canopy, sub-canopy and understorey (Kress and Beach, 1994) recorded the highest values of dioecy among canopy (24.5 %) rather than understorey species (9.8 %). Sobrevila and Arroyo (1982) also recorded a marked difference between the values of dioecy among trees (30.55 %) and shrubs, herbs and vines (2.56 %). In the Caatinga areas, three of the four dioecious species are trees and one (*Clusia nemorosa*) is a shrub, although this latter species usually occurs as a tree in the Brazilian Amazonian and Atlantic forests. Thus, as mentioned above, the percentage of dioecy among trees in the present study is 11 % (three out of 28 tree species), or 14.3 % if *Clusia nemorosa* is included.

Breeding system studies

The 39 species for which breeding system studies are available (Table 3) belong to 13 families, including the three most common in Caatinga communities, Cactaceae, Euphorbiaceae and Leguminosae. Analysis revealed a high percentage of self-incompatible (SI) species (61.5 %) represented by 24 species, including the six heterostylous ones [*Auxemma glazioviana*, *A. oncocalyx*, *Cordia globosa*, *C. leucocephala* (Boraginaceae), *Melochia tomentosa* and *Waltheria rotundifolia* (Sterculiaceae)]. The percentage of self-compatibility (SC) was 38.5 %, recorded for 15 species of which seven species set fruit after spontaneous self-pollination. Agamospermy was not recorded in the Caatinga species studied. A similar low (or null) level of agamospermy was recorded for other tropical communities, both dry (Bawa, 1974; Ruiz-Zapata and Arroyo, 1978; Bullock, 1985) or humid (Ramírez and Seres, 1994). The high frequency (15.38 %) of agamospermy in a morichal community was associated with inappropriate pollinators (Ramírez and Brito, 1990). These authors also drew attention to the incidence of agamospermy in some Melastomataceae (see review by Renner, 1989), a family which was not represented in the present study.

The high frequency of SI species in the Caatinga is similar to records by Oliveira and Gibbs (2000) for a Cerrado community in Brazil, and also to other dry (Bawa, 1974; Bullock, 1985) and humid (Bawa *et al.*, 1985) tropical forest communities (Table 2). Although SI has been reported as predominant in tropical communities (Bawa *et al.*, 1985; Jaimes and Ramírez, 1998), higher frequencies of SC in relation to SI species were reported by Sobrevila and

Arroyo (1982) for a Venezuelan montane forest (26.21 % of SI considering trees only or 41.76 % of SI for shrubs, herbs and vines), by Ramírez and Brito (1990) for a palm swamp community also in Venezuela (30.77 % of SI species) and by Tanner (1982) for a Jamaican montane forest (12 %) (Table 2).

Although the frequency of SI species was similar to other forests, the level of SI plus the frequency of dioecy in the Caatinga gives a smaller frequency of obligate outcrossing species for this community in comparison, for example, with the Cerrado studied by Oliveira and Gibbs (2000) with 66 % SI species and 15 % with dioecy, a total of 81 % of obligatory outcrossing species. However the frequency of total obligate outcrossing species in the Caatinga (61.5 SI + 2.7 dioecy), even with a low level of dioecy, is still higher than some humid ecosystems showed in Table 2, such as a tropical palm swamp (Ramírez and Brito, 1990) and a montane cloud forest (Sobrevila and Arroyo, 1982), both in Venezuela, and a Jamaican montane forest (Tanner, 1982).

With regard to the habit of the 39 species with breeding system data (Table 3), high frequencies of SI species predominate in all woody life forms (80 % of the tree species, 63.2 % of the shrubs, 75 % of the lianas), but less so in herbs (28.6 %). The herbaceous annual habit has been associated with self-compatibility (Stebbins, 1950), and it is of interest to note that the two herbaceous species with SI in the present survey are in fact perennial species.

The relatively small sample of species in this study indicates that high levels of SI seem to predominate in Caatinga species independent of taxonomic affinities, thus making cross-pollination services of great importance for this ecosystem, as proposed for the Cerrados (Oliveira and Gibbs, 2000) and tropical rain forests (Bawa *et al.*, 1985). More studies concerning the breeding and incompatibility systems of Caatinga species are needed to verify what types of reproductive mechanisms occur in plant species of this ecosystem.

ACKNOWLEDGEMENTS

We are grateful to P. E. Gibbs (University of St Andrews, Scotland) and S. Bullock (University of San Diego, USA) for critically reading the first drafts of the manuscript and also for kindly improving the English, also to S. Vogel (University of Vienna, Austria) for fruitful discussions. The Curators and Taxonomists of the Herbaria UFP, IPA and PEUFR and the taxonomists F. Agra (UFPB), G. S. Baracho (UFPE), L. P. Felix (UFPB), I. B. Loiola (UFRN), L. Paganucci (UEFS), R. Pereira (IPA), J. Semir (UNICAMP), J. A. Siqueira-Filho (UFPE), V. Souza (Esalq-USP) and D. Zappi (Kew Gardens) for identifying most of the plant species. Three referees (P. Gibbs, P. Oliveira and one anonymous) for several relevant improvements in the manuscript. Also to A. V. L. Leite for unpublished data, and the owners/administrators of the study sites for permission to carry out our studies at areas under their care. The UFPE, CNPq, FACEPE, CAPES, for essential financial support.

LITERATURE CITED

- Aguiar J, Lacher T, Silva JMC. 2002. The Caatinga. In: Gil PR, ed. *Wilderness—Earth's last wild places*. Mexico City: CEMEX, 174–181.
- Anderson GJ, Symon DE. 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204–219.
- Baker HG. 1959. Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harbor Symposium on Quantitative Biology* 24: 177–191.
- Barbosa AAA. 1997. *Biologia reprodutiva de uma comunidade de Campo sujo, Uberlândia/MG*. Tese de Doutorado, Universidade Estadual de Campinas, Campinas.
- Bawa KS. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* 28: 85–92.
- Bawa KS. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11: 15–39.
- Bawa KS. 1990. Plant–pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21: 399–422.
- Bawa KS, Hadley M. 1990. *Reproductive ecology of tropical forest plants*. Carnforth: Parthenon.
- Bawa KS, Opler PA. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167–179.
- Bawa KS, Perry DR, Beach JH. 1985. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. *American Journal of Botany* 72: 331–345.
- Bezerra ELS. 2004. *Polinização e fenologia reprodutiva de Byrsonima gardneriana Juss. e Stigmaphyllon paralias Juss. (Malpighiaceae) em área de Caatinga, Nordeste do Brasil*. Dissertação de Mestrado, Universidade Federal de Pernambuco, Recife.
- Bullock SH. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica* 17: 287–301.
- Bullock SH. 1995. Plant reproduction in neotropical dry forests. In: Bullock SH, Mooney HA, Medina E, eds. *Seasonally dry tropical forests*. Cambridge: Cambridge University Press, 277–303.
- Coleman JR, Coleman MA. 1982. Reproductive biology of an andromonoecious *Solanum* (*S. palinacanthum* Dunal). *Biotropica* 14: 69–75.
- Croat TB. 1979. The sexuality of the Barro Colorado Island flora (Panama). *Phytologia* 42: 319–348.
- Dafni A, O'Toole C. 1994. Pollination syndromes in the Mediterranean: generalizations and peculiarities. In: Arianoutsou M, Groves RH, eds. *Plant–animal interactions in Mediterranean-type ecosystems*. Amsterdam, The Netherlands: Kluwer Academic Publishers, 125–135.
- Egler WA. 1951. Contribuição ao estudo da Caatinga Pernambucana. *Revista Brasileira de Geografia* 13: 577–590.
- Enrech NX, Ramírez N, Sobrevila C. 1988. Notas sobre la dinámica reproductiva de una comunidad vegetal tropical de vega de río. *Actes del Simposi Internacional de Botànica Pius Font i Quer 2 (Fanerogàmia)*: 69–82.
- Federov AA. 1966. The structure of the tropical rain forest and speciation in the humid tropics. *Journal of Ecology* 54: 1–11.
- Ferraz EM, Rodal MJN, Sampaio EVSB, Pereira RCA. 1998. Composição florística em trechos de vegetação de Caatinga e Brejo de Altitude na região do Vale do Pajeú, Pernambuco. *Revista Brasileira de Botânica* 21: 7–15.
- Figueiredo LS, Rodal MJN, Melo AL. 2000. Florística e fitossociologia de uma área de vegetação arbustiva caducifolia espinhosa no município de Buíque—Pernambuco. *Naturalia* 25: 205–224.
- Flores S, Schemske DW. 1984. Dioecy and monoecy in the flora of Puerto Rico and the Virgin Islands: ecological correlates. *Biotropica* 16: 132–139.
- Fox JF. 1985. Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia* 67: 244–249.
- Gibbs PE. 1990. Self-incompatibility in flowering plants: a neotropical perspective. *Revista Brasileira Botânica* 13: 125–136.
- Gil PR (ed.). 2002. *Wilderness—earth's last wild places*. Mexico City: CEMEX.
- Griz LMS, Machado IC. 2001. Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology* 17: 303–321.

- Hueck K. 1972. A região da caatinga do Nordeste brasileiro. In: *As florestas da América do Sul*. São Paulo: Ed. Universidade de Brasília e Ed. Polígono S.A., 306–327.
- Ibarra-Manriquez G, Oyama K. 1992. Ecological correlates of reproductive traits of Mexican rain forest trees. *American Journal of Botany* 79: 383–394.
- Jaimes I, Ramírez N. 1998. Autoincompatibilidad, autogamia y agamospermia en angiospermas tropicales. *Acta Biologica Venezuelana* 18: 59–80.
- Kato M. 1996. Plant–pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany* 83: 732–743.
- Kiill LHP, Drummond MA. 2001. Biologia floral e sistema reprodutivo de *Gliricidia sepium* (Jacq.) Steud. (Fabaceae- Papilionoidae) na região de Petrolina, Pernambuco. *Ciência Rural* 31: 597–601.
- Kiill LHP, Ranga NT. 2000a. Biologia da polinização de *Merremia aegyptia* (L.) Urb. (Convolvulaceae) no Sertão de Pernambuco. *Naturalia* 25: 149–158.
- Kiill LH, Ranga NT. 2000b. Biologia floral e sistema de reprodução de *Jacquemontia multiflora* (Choisy) Hallier f. (Convolvulaceae). *Revista Brasileira de Botânica* 23: 37–43.
- Kiill LHP, Ranga, NT. 2003. Ecologia da polinização de *Ipomoea asarifolia* (Ders.) Roem. & Schult. (Convolvulaceae) na região Semi-árida de Pernambuco. *Acta Botanica Brasílica* 17: 355–362.
- Kress WJ, Beach JH. 1994. Flowering plant reproductive systems. In: McDade LA, Bawa KS, Hespdenheide H, Hartshorn G, eds. *La Selva: ecology and natural history of a neotropical rain forest*. Chicago, IL: University of Chicago Press, 161–182.
- Leal IR, Tabarelli M, Silva JMC. 2003. *Ecologia e conservação da Caatinga*. Recife: Editora Universitária.
- Lewis G, Gibbs P. 1999. Reproductive biology of *Caesalpinia calycina* and *C. pluviosa* (Leguminosae) of the Caatinga of north-eastern Brazil. *Plant Systematics and Evolution* 217: 43–53.
- Locatelli E, Machado IC. 1999. Comparative study of the floral biology in two ornithophilous species of Cactaceae: *Melocactus zehntneri* and *Opuntia palmadora*. *Bradleya* 17: 75–85.
- Lopes AV, Machado ICS. 1998. Floral biology and reproductive ecology of *Clusia nemorosa* (Clusiaceae) in northeastern Brazil. *Plant Systematics and Evolution* 213: 71–90.
- Machado ICS. 1990. *Biologia floral de espécies de caatinga no município de Alagoinha (PE)*. Tese de Doutorado, Universidade Estadual de Campinas, Campinas.
- Machado ICS. 1996. Biologia floral e fenologia. In: Sampaio EVSB, Mayo SJ, Barbosa MRV, orgs. *Pesquisa Botânica Nordestina: Progresso e Perspectivas*. Recife: Sociedade Botânica do Brasil-Seção Regional de Pernambuco e Editora Universitária, 161–172.
- Machado IC, Lopes AV. 2002. A Polinização em ecossistemas de Pernambuco: uma revisão do estado atual do conhecimento In: Tabarelli M, Silva JMC, orgs. *Diagnóstico da Biodiversidade de Pernambuco*. Recife: Secretaria de Ciência Tecnologia e Meio-Ambiente, Fundação Joaquim Nabuco e Editora Massangana, 583–596.
- Machado IC, Lopes AV. 2004. Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry forest. *Annals of Botany* 94: 365–376.
- Machado ICS, Sazima M. 1995. Biologia da polinização e pilhagem por beija-flores em *Ruellia asperula* Lindau (Acanthaceae) na Caatinga de Pernambuco. *Revista Brasileira de Botânica* 18: 27–33.
- Machado ICS, Barros LM, Sampaio EVSB. 1997. Phenology of Caatinga species at Serra Talhada, PE, Northeastern Brazil. *Biotropica* 29: 57–68.
- Machado IC, Vogel S, Lopes AV. 2002. Pollination of *Angelonia cornigera* Hook. (Scrophulariaceae) by long-legged, oil-collecting bees in NE Brazil. *Plant Biology* 4: 352–359.
- Matallana G, Wendt T, Araujo DSD, Scarano FR. 2005. High abundance of dioecious plants in a tropical coastal vegetation. *American Journal of Botany* 92: 1513–1519.
- MMA 2002. *Avaliação e ações prioritárias para a conservação da biodiversidade da Caatinga*. Universidade Federal de Pernambuco/ Fundação de Apoio ao Desenvolvimento/ Conservation International do Brasil, Fundação Biodiversitas, EMBRAPA/Semi-Árido. Brasília, MMA/SBF.
- Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, et al. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant–pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85: 1477–1501.
- Oliveira PE, Gibbs PE. 2000. Reproductive biology of woody plants in a Cerrado community of Central Brazil. *Flora* 195: 311–329.
- Ormond WT, Pinheiro MCB, De Castells ARC. 1984. Contribuição ao estudo da reprodução e biologia floral de *Jatropha gossypifolia* L. (Euphorbiaceae). *Revista Brasileira de Biologia* 44: 159–167.
- Ormond WT, Pinheiro MCB, Lima HA. 1991. Sexualidade das plantas da restinga de Maricá, RJ. *Boletim do Museu Nacional do Rio de Janeiro, Série Botânica* 87: 1–24.
- Piedade LH. 1998. *Biologia da polinização e reprodutiva de sete espécies de Convolvulaceae na Caatinga do sertão de Pernambuco*. Tese de Doutorado, Universidade Estadual de Campinas, Campinas.
- Pinheiro MCB, Ormond WT, Castro AC. 1991. Biologia da reprodução e fenologia de *Zizyphus joazeiro* Mart. (Rhamnaceae). *Revista Brasileira de Biologia* 51: 143–152.
- Primo LM. 2004. *Biologia floral e reprodutiva de Capparis jacobinae Moric. ex Eichler e Capparis hastata L. (Capparaceae)*. Dissertação de Mestrado, Universidade Federal de Pernambuco Recife.
- Quirino ZGM, Machado ICS. 2001. Biologia da polinização e da reprodução de três espécies de Combretum Loebl. (Combretaceae). *Revista Brasileira de Botânica* 24: 181–193.
- Ramírez N, Brito Y. 1990. Reproductive biology of a tropical palm swamp community in the Venezuelan Llanos. *American Journal of Botany* 77: 1260–1271.
- Ramírez N, Seres A. 1994. Plant reproductive biology of herbaceous monocots in Venezuelan tropical cloud forest. *Plant Systematics and Evolution* 190: 129–142.
- Ramírez N, Gil C, Hokche O, Seres A, Brito Y. 1990. Biologia floral de una comunidad arbustiva tropical en la Guayana Venezolana. *Annals of the Missouri Botanical Garden* 77: 383–397.
- Renner SS. 1989. A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. *Annals of the Missouri Botanical Garden* 76: 469–518.
- Renner S, Ricklefs R. 1995. Dioecy and its correlates in the flowering plants. *American Journal of Botany* 82: 596–606.
- Richards AJ. 1986. *Plant breeding systems*. London: George Allen & Unwin.
- Rodal MJN, Melo AL. 1999. Levantamento preliminar das espécies lenhosas da Caatinga de Pernambuco. *Anais I Workshop Geral Programa Plantas do Nordeste*. Kew: Royal Botanic Gardens, 53–62.
- Rodal MJN, Andrade KVA, Sales MF, Gomes APS. 1998. Fitossociologia do componente lenhoso de um refúgio vegetal na Caatinga do município de Buíque, Pernambuco. *Revista Brasileira de Biologia* 58: 517–526.
- Ruiz-Zapata T, Arroyo MTK. 1978. Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica* 10: 221–230.
- Sampaio EVSB. 1995. Overview of the Brazilian caatinga. In: Bullock SH, Mooney HA, Medina E, eds. *Seasonally dry tropical forests*. Cambridge: Cambridge University Press, 35–63.
- Santos MJ, Machado IC, Lopes AV. 2005. Ecologia da polinização e fenologia de duas espécies de *Jatropha* L. (Euphorbiaceae) ocorrentes em Caatinga, Pernambuco, Nordeste do Brasil. *Revista Brasileira de Botânica* 28: 361–373.
- Saraiva LC, Cesar O, Monteiro R. 1996. Breeding systems of shrubs and trees of a Brazilian savanna. *Arquivos de Biologia e Tecnologia* 39: 751–763.
- Silva AG, Guedes-Bruni RR, Lima MPM. 1997. Sistemas sexuais e recursos florais do componente arbustivo-arbóreo em mata preservada na reserva ecológica de Macaé de Cima. In: Lima HC, Guedes-Bruni RR, orgs. *Serra de Macaé de Cima: Diversidade Florística e Conservação em Mata Atlântica*. Rio de Janeiro: Jardim Botânico, 187–211.

- Silva AMP, Machado IC. 1997.** Biologia da reprodução e morfologia polínica de *Auxemma* Miers (Boraginaceae). *Boletim da Sociedade Broteriana* **68**: 73–88.
- Silva VC. 2004.** *Biologia floral e sistema reprodutivo de duas espécies de Chamaecrista (Leguminosae) ocorrentes em Buíque, Pernambuco*. Dissertação de Mestrado, Universidade Federal de Pernambuco, Recife.
- Sobrevila C, Arroyo MTK. 1982.** Breeding systems in a Montane Tropical Cloud Forest in Venezuela. *Plant Systematics and Evolution* **140**: 19–37.
- Stebbins GL. 1950.** *Variation and evolution in plants*. New York, NY: Columbia University Press.
- Steiner KM. 1988.** Dioecism and its correlates in the Cape flora of South Africa. *American Journal of Botany* **75**: 1742–1754.
- SUDENE. 1990.** *Dados pluviométricos do Nordeste—Estado de Pernambuco*. Série Pluviométrica 6. Recife: Superintendência do Desenvolvimento do Nordeste (SUDENE).
- Symon DE. 1979.** Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects. In: Hawkes JG, Lester RN, Skelding AD, eds. *The biology and taxonomy of the Solanaceae*. Linnean Society Symposium Series 7. London: Academic Press.
- Tabla VP, Bullock S. 2002.** La polinización en la selva tropical de Chamela. In: Noguera FA, Rivera JHV, Aldrete ANG, Avendaño MQ, eds. *História natural de Chamela*. Mexico: Instituto de Biología, UNAM, 499–515.
- Tanner EV. 1982.** Species diversity and reproductive mechanisms in Jamaican trees. *Biological Journal of the Linnean Society* **18**: 263–278.
- Vogel S, Machado IC. 1991.** Pollination of four sympatric species of *Angelonia* (Scroph.) by oil-collecting bees in NE Brazil. *Plant Systematics and Evolution* **178**: 153–178.
- Vogel S, Machado IC, Lopes AV. 2004.** *Harpochilus neesianus* and other novel cases of chiropterophily in neotropical Acanthaceae. *Taxon* **53**: 55–60.
- Wesselingh R, Witteveldt M, Morissette J, Nijs HCM den. 1999.** Reproductive ecology of understory species in a tropical montane forest in Costa Rica. *Biotropica* **31**: 637–645.